

LIFE HISTORY OF THE EUROPEAN TEPHRITID FLY *CHAETOSTOMELLA CYLINDRICA* (DIPTERA: TEPHRITIDAE) AND ITS POSSIBLE USE AS A BIOCONTROL AGENT IN THE USA

JUDITA KINKOROVÁ AND MICHAELA MÍČKOVÁ

Department of Zoology, Charles University, Viničná 7, CZ—128 44 Praha 2, Czech Republic (e-mail: kinkor@natur.cuni.cz)

Abstract.—*Chaetostomella cylindrica* (Robineau-Desvoidy) is a polyphagous fly widely distributed in most of Europe. Its life history, with emphasis on the previously unknown developmental stages, and reproductive behavior, is described. The development of *C. cylindrica* was followed on the knapweed *Centaurea pseudophrygia* C.A.Meyer (Asteraceae) that has been introduced to the USA and is likely to become a serious menace to agriculture. *Chaetostomella cylindrica* attacks a number of other introduced knapweeds and thistles (a complete list of host plants is provided) but destroys only 1–3 achenes in the flowerheads. Reproductive potential of the infested host plants must be examined to assess the possible use of *C. cylindrica* in weed biocontrol.

Key Words: fruit fly, *Chaetostomella cylindrica*, life history, behavior, knapweed, weed biocontrol

Certain tephritid species (Diptera: Tephritidae) have proved to be effective biological control agents of noxious weeds introduced from Europe to North America. Currently seven tephritid species have been established to curb thistles and knapweeds of European origin in the USA and Canada. Several thistles and knapweeds, e.g., *Carduus nutans* L., *Cirsium arvense* (L.) Scopoli, and *Centaurea maculosa* Lam., that are suitable candidates for biological control by fruit flies (Harris and Myers 1984) are host to *Chaetostomella cylindrica*, (Robineau-Desvoidy) a common fly species in Europe (Kinkorová 1999). The genus *Chaetostomella* Hendel, 1927 (subfamily Tephritinae, tribe Terelliini) includes 14 species worldwide (Norrbom et al. 1998a), 12 of them from the Palearctic and one from the Oriental Region. The remaining species, *C. undosa* (Coquillett), is native to the Nearctic Region; its immature stages, life history,

and host plant range were described by Steck (1984). The eastern Palearctic has nine species and is obviously the center of origin for the genus (Steck 1984).

Chaetostomella cylindrica has been reported to infest a number of plant species belonging to at least ten genera of the Cardueae (Table 1). The life history and the immature stages of *C. cylindrica* were to some extent described by Hendel (1927), Varley (1937), Leclercq (1967), Dirlbek (1970), and Kugler and Freidberg (1975). However, a number of important aspects of both its morphology and biology have not been examined and are lacking in the latest review published by White (1988). A more complete examination of *C. cylindrica* became imperative with the prospect of using it as a biological control agent in North America. Knowledge of the life history and positive determination of both the immatures and adults are necessary to assess the

Table 1. Host plants of *Chaetostomella cylindrica* mentioned in the literature.

Author	Host Plants
Freidberg and Kugler 1989	<i>Onopordon cynarocephalum</i> , <i>O. floccosum</i> , <i>Cousinia hermonis</i> , <i>Cirsium gaillardotii</i> , <i>Echinops viscosus</i>
Kinkorová 1999	Cardueae
Merz 1994	<i>Arctium lappa</i> , <i>A. tomentosum</i> , <i>Carduus crispus</i> , <i>C. nutans</i> , <i>Centaurea bracteata</i> , <i>C. cyanus</i> , <i>C. dubia</i> , <i>C. jacea</i> , <i>C. maculosa</i> , <i>C. montana</i> , <i>C. nervosa</i> , <i>C. nigra</i> , <i>C. scabiosa</i> , <i>C. triumfetti</i> , <i>Cichorium intybus</i> , <i>Cirsium arvense</i> , <i>C. eriophorum</i> , <i>C. erisithales</i> , <i>C. heterophyllum</i> , <i>C. oleraceum</i> , <i>C. paulustre</i> , <i>C. rivulare</i> , <i>C. tuberosum</i> , <i>C. vulgare</i> , <i>Crupina vulgaris</i> , <i>Jurinea mollis</i> , <i>Onopordum acanthium</i> , <i>Serratula tinctoria</i>
Richter 1970	<i>Arctium lappa</i> , <i>A. tomentosum</i> , <i>Centaurea calcitrapa</i> , <i>C. cyanus</i> , <i>C. jacea</i> , <i>C. maculosa</i> , <i>C. montana</i> , <i>C. phrygia</i> , <i>C. pseudophrygia</i> , <i>C. scabiosa</i> , <i>C. solstitialis</i> , <i>Carduus acanthoides</i> , <i>C. crispus</i> , <i>Cirsium canum?</i> , <i>C. eriophorum</i> , <i>C. vulgare</i> , <i>C. oleraceum</i> , <i>C. palustre</i> , <i>Jurinea mollis</i> , <i>Carthamus dentatus</i> , <i>Onopordum</i> , <i>Serratula tinctoria</i>
White 1988	Great Britain: <i>Centaurea montana</i> , <i>C. nigra</i> , <i>Cirsium arvense</i> , <i>C. palustre</i> , <i>Serratula tinctoria</i> , ? <i>Centaurea debeauxii</i> , ? <i>Cirsium dissectum</i> France: <i>Carduus acanthoides</i> , <i>C. nutans</i> , <i>C. jacea</i> , <i>C. montana</i> , <i>C. scabiosa</i> , <i>C. solstitialis</i> , <i>Cirsium acaulon</i> , <i>C. eriophorum</i> , <i>C. pycnocephalus</i> , <i>Centaurea calcitrapa</i> , <i>C. cyanus</i> , <i>C. debeauxii</i> , <i>helenioides</i> , <i>C. oleraceum</i> , <i>C. palustre</i> , <i>C. tuberosum</i> , <i>Onopordum acanthium</i> , ? <i>Cirsium eriophorum</i> , ? <i>C. vulgare</i> , ?? <i>Arctium lappa</i> , ?? <i>A. tomentosum</i> , ?? <i>Sonchus asper</i> , ?? <i>Taraxacum officinale</i>

potential of *C. cylindrica* as a biocontrol agent and, if used, to monitor its post-release populations and to distinguish it from *C. undosa* native to North America.

This study concerns little known aspects of *C. cylindrica* bionomics, with emphasis on the reproductive behavior. The study was done on flies living on the knapweed *Centaurea pseudophrygia* C. A. Meyer. This host plant was inadvertently introduced in to the USA where it is usually referred to as *Centaurea phrygia* L. It has been reported from Ohio, Vermont, and New York, but its occurrence in New York requires confirmation (www.csd1.tamu.edu/FLORA). This knapweed is likely to spread as a weed and *C. cylindrica* should be considered as a potential biocontrol agent that also could curb a number of other invasive knapweeds and thistles.

MATERIALS AND METHODS

Collection of specimens.—Field observations and laboratory studies were conducted in 2001 through 2003. *Chaetosto-*

mella cylindrica was observed and collected at three localities in the northwestern part of Bohemia (Czech Republic), near Litvínov in the Krušné hory Mts, at an altitude of ca. 420 to 460 m. The sites, each about 4,000 m² in size, were orientated southeast and situated in a deciduous forest with high abundance of the host plant, *Centaurea pseudophrygia*. Flies collected on several other host plants in a dozen localities near Prague (central Bohemia) were used for morphological comparison. As no differences were found, the data on these additional collections are not included in this publication.

The study sites were visited every 10 to 14 days from April to October to observe the emergence of adults, their pre mating and mating behavior, oviposition, and other aspects of their biology. Phenological phases of the host plant, *C. pseudophrygia*, were recorded. Flies were both swept or reared from the host plants and taken to the laboratory. Samples of buds and flower heads were dissected, and the eggs, larvae and pu-

pae preserved in 75% ethanol for scanning electron microscopy. The numbers of eggs, developing larvae, and pupae were counted in randomly chosen flower heads (300 in each sample). Special attention was given to the damage inflicted by the larvae, to the achenes and other flower head tissues.

Both swept and reared adults were used to study reproductive behavior. Males and females (one or two pairs) were placed in a glass cage (0.75 l) together with a knapweed plant in the appropriate stage of bud development, a paper strip with artificial diet (water, honey, sugar and yeast), and a cotton-plugged water vial. Precopulatory, copulatory and oviposition behaviors were observed, described and recorded. The buds with newly oviposited eggs were dissected and recorded.

Scanning electron microscopy (SEM).—The specimens fixed in 75% ethanol for scanning electron microscopy were dehydrated through an increasing series of acidulated ethanol to 100%, critical-point dried, mounted on stubs, and sputter coated with a gold-palladium alloy. The specimens were studied with a JEOL JSM 6400 scanning electron microscope in the microscopy center of the Institute of Macromolecular Chemistry, Academy of Sciences of the Czech Republic, Prague.

Host plant.—Plant names used in this paper follow Kubát et al. (2002). Tutin (1976) and some other botanists distinguished two closely related *Centaurea* species named *C. phrygia* and *C. pseudophrygia*, but recent data revealed that it is a single species which should be referred to as *C. pseudophrygia*; all other botanical names are considered as synonyms (Kubát et al. 2002). Characteristic features of *C. pseudophrygia* include: stems up to more than 100 cm and more or less branched; leaves green, scabrid, rarely sparsely arachnoid-hairy beneath, oblong-lanceolate to ovate, acuminate; capitula solitary or in clusters of 2–4; florets pinkish purple, the outer radiate. The known distribution is throughout Europe and the southern parts of the former

U.S.S.R., and was recently introduced to the USA.

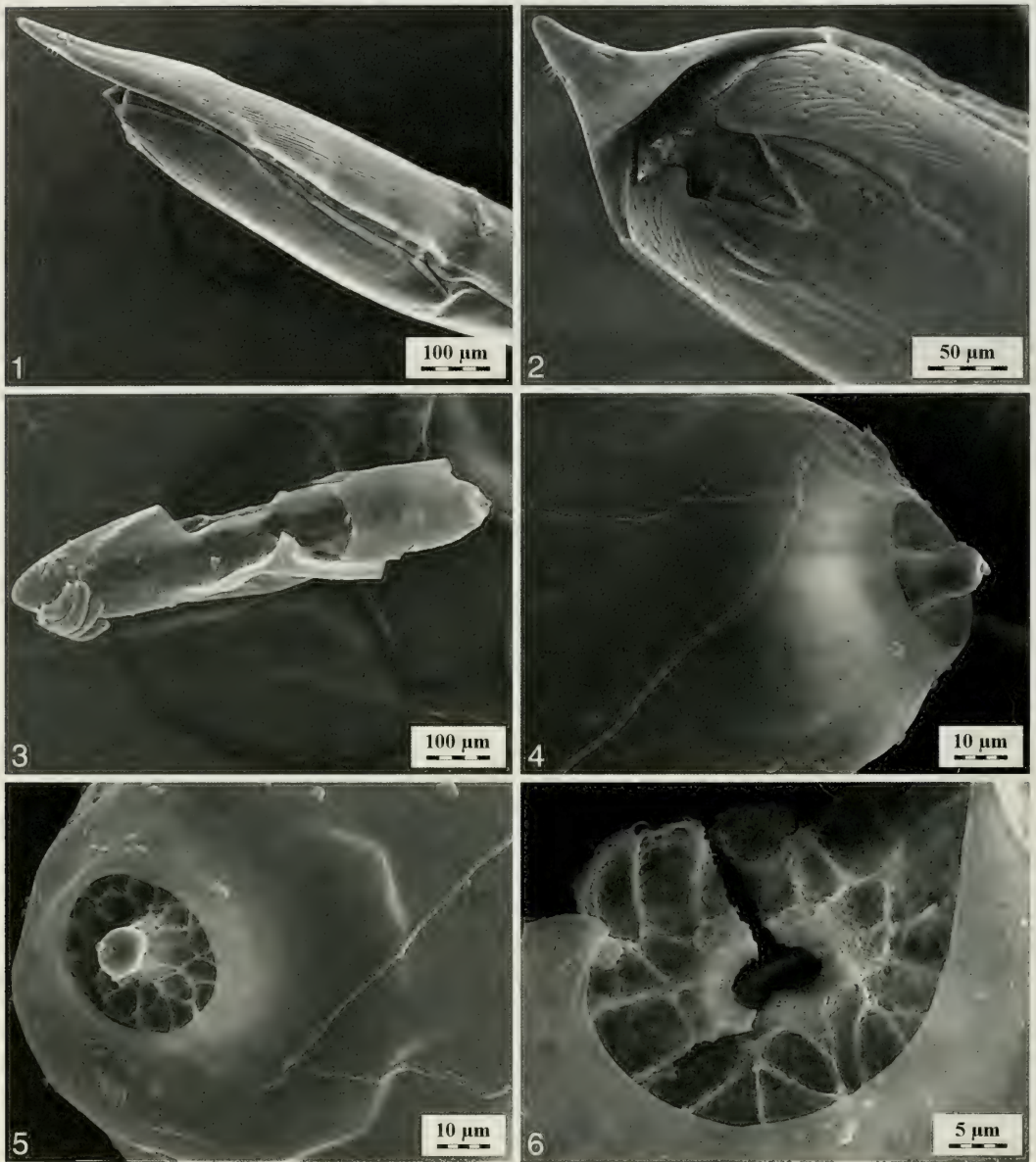
Terminology and vouchered specimens.—Tephritid classification can be found in Norrbom et al. (1998b), terminology used in larval and pupal descriptions in White and Elson-Harris (1992), and terminology describing the behavior and wing displays in Headrick and Goeden (1994). Voucher specimens of immature and adult stages are stored in the collection of Charles University, Prague.

RESULTS AND DISCUSSION

Taxonomy

Adult.—*Chaetostomella cylindrica* was first described by Robineau-Desvoidy (1830) as *Tephritis cylindrica*. In the older literature the species can be found as *Trypeta onotrophes* Loew 1846, and later *Chaetostomella onotrophes* Loew. Full synonymy is in Thompson (1998).

The adult of *C. cylindrica* can be distinguished easily from other Terelliinae by the wing pattern. The wing has four yellow to brownish-bordered crossbands: basal and discal, preapical, and apical. The latter two bands are connected along costal wing margin; whereas discal and preapical crossbands are clearly separate; the body is yellow, the mesoscutum with the typical terelliinae dark lyre-shaped pattern, and the prescutellar dorsocentral setae inserted on a black spot. The scutellum is yellow with a distinct apical and two lateral spots; and two pairs of scutellar setae. The only species that could be mistaken for *C. cylindrica* in central Europe is the monophagous *C. rossica* Hendel, but the two species differ in the color of the postocular bristles, which are whitish in *C. cylindrica* and reddish in *C. rossica*. *Chaetostomella rossica* occurs in southeastern Europe and the Ukraine but has not yet been reported from the Czech Republic, where its host plant, *Jurinea mollis* (L.) Reichenb., grows in the region of southern Moravia (Kinkorová and Chvála 2000).

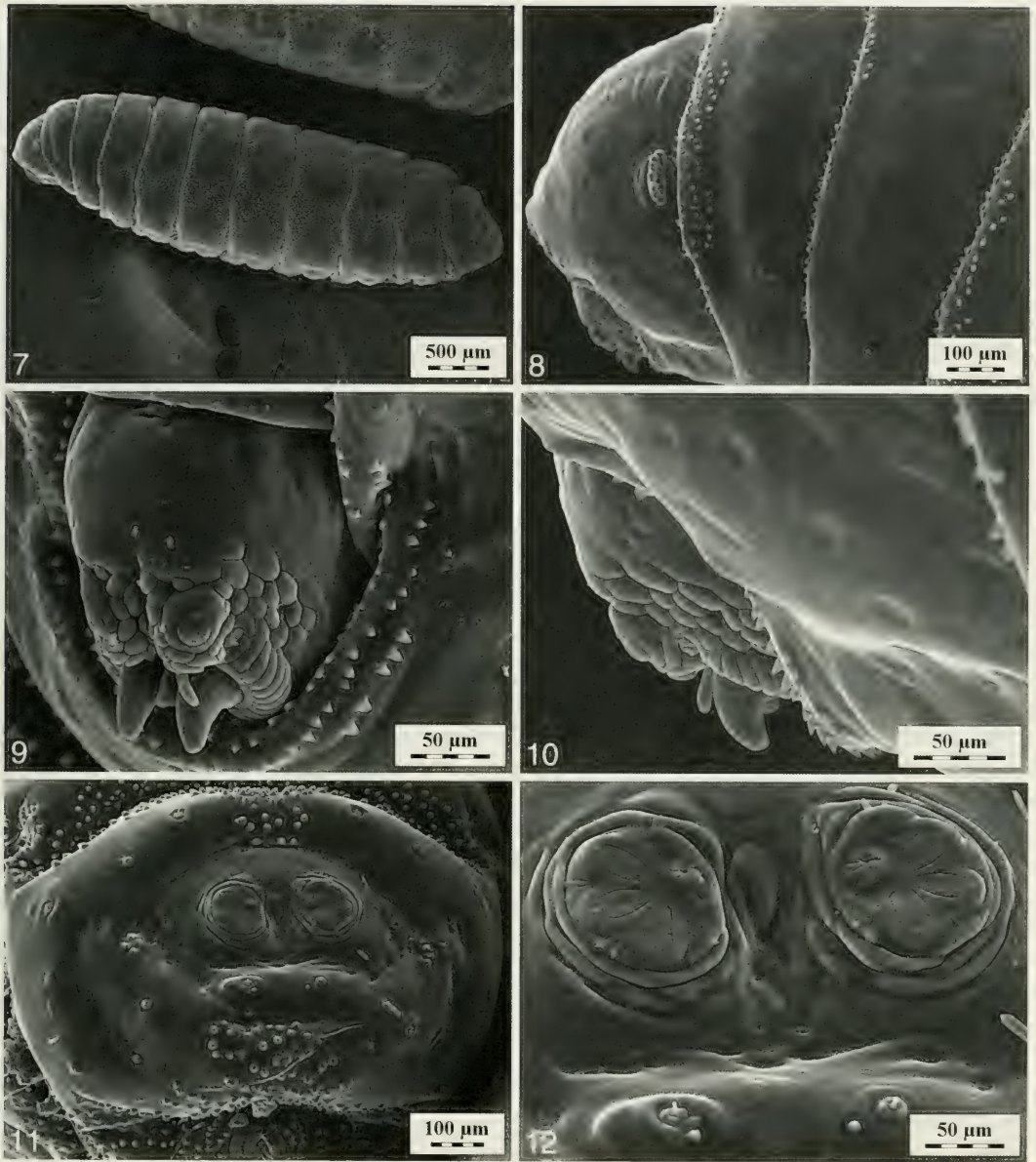


Figs. 1–6. *Chaetostomella cylindrica*. 1, Tip of ovipositor with egg inside, lateral view. 2, Tip of ovipositor with egg inside, ventral view. 3, Egg. 4, Apical part of egg with pedicel and micropyle, lateral view. 5, Apical part of egg with pedicel and micropyle, anterior end. 6, Apical part of micropyle of egg without pedicel, anterior end.

Immature stages.—The immature stages of *C. cylindrica* are similar to those described for *C. undosa* by Steck (1984). The line drawings of Steck (1984) have a limited resolution in comparison to the scanning electron microphotographs, but even

with this refined technique it may not be possible to distinguish the immature stages of the two species from one another.

In *C. cylindrica*, the egg (Figs. 3–6) is smooth and white, 0.76 ± 0.006 mm ($n = 8$) long and 0.20 ± 0.001 mm wide, oval,



Figs. 7–12. Third-instar larva. 7, Lateral view. 8, Gnathocephalon with anterior thoracic spiracles. 9, Gnathocephalon, dorsal sensory organ, mouth hooks, oral ridges. 10, Gnathocephalon, lateral view: mouth hooks, anterior sensory organ, oral ridges. 11, Caudal segment with posterior spiracular plates. 12, Caudal segment with posterior spiracular plates and sensillae.

and gently tapering at the posterior end. The buttonlike pedicel (Figs. 4–5) is at the apex of a short, tubular extension in the middle of a finely sculptured aeropylar area (Fig. 6) with a diameter of 0.025 ± 0.002 mm.

The fully grown third-instar larva (Figs. 7–12), is 3.95 ± 0.04 mm ($n = 10$) long, with a maximal width of 1.68 ± 0.03 mm. The body is creamy whitish, maggot like in shape, with the caudal segment slightly truncate and the thoracic segments tapered

toward the anterior gnathocephalon (Fig. 8). Body segments (thoracic and abdominal) are smooth with irregular rows of rounded projections and spinules. The head segment is bilobate anteriorly with a pair of sensory lobes bearing several sensory organs (Figs. 9–10). The mouth opening is situated ventrad on the gnathocephalon between the two distinct sclerotised mouthhooks; median oral lobe is flattened. The mouth opening is surrounded with rugose pentagonal pads on its anterior margin and with an oral ridge area bearing rib like plates on the lateral margin. The anterior spiracles (Fig. 8) are situated dorsolaterally on each side of the prothoracic segment and bear an inconsistent number of rounded papillae, usually from 6 to 9. The caudal pentagonal-shaped segment consists of a spiracular area and the anal elevation (Figs. 11–12). The spiracular area bears two posterior spiracular plates each with three rimae 0.04 mm long (Fig. 12), and four interspiracular processes that are each 3-branched, and medially. The ecdysial scar is situated medially on the posterior spiracular plate. The caudal plate is surrounded by pairs of dorsal, lateral and ventral sensoria composed of stelex and medusoid sensilla (Fig. 12).

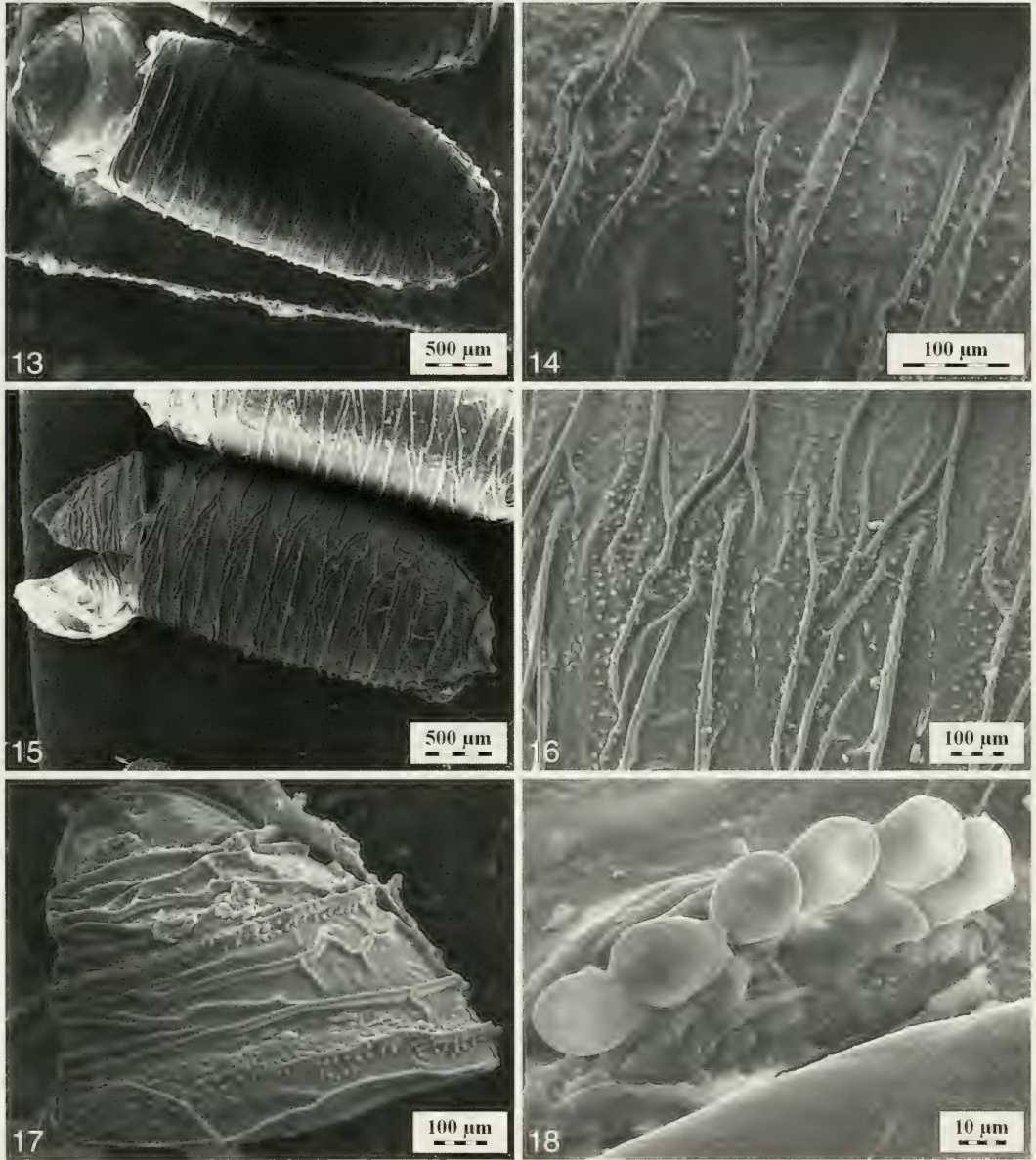
The puparium (Figs. 13–20) is 3.75 ± 0.05 mm long ($n = 15$), maximal width 1.55 ± 0.04 mm, oval shaped, brownish and well sclerotized. The whole surface is circumscribed with numerous transverse ribs indicating the inner segmentation and with numerous projections or acanthae (Figs. 14–16). The anterior end bears the invagination scar and anterior thoracic spiracles which protrude from the puparial surface (Figs. 17–18). The caudal plate is pentagonal, darkly pigmented, with distinct spiracular area (Figs. 19–20). Each posterior spiracular plate bears an ecdysial scar, three oval rimae, and four interspiracular processes each three branched. Several sensoria composed of stelex and medusoid sensilla are regularly situated around the spiracular plates on the surface of the caudal plate.

Figs. 21–22 demonstrate how the adult opens the puparium through the evagination scar, the position of the anterior plates of the puparium after emergence, with respect to the anterior thoracic spiracle.

Biology

Adults first appeared at the study sites on 11 May 2002, and within 3 weeks females were laying eggs. Each egg was deposited between developing florets with its caudal part embedded in the receptacle and the pedicel facing upward. The newly hatched larva tunneled down through the florets to the developing achenes and receptacle. The first and second instar larvae fed on achenes. One to three larvae occupied one flower head; more were found on rare occasions, but in these cases some failed to complete their development. If more than a single larva was developing in the flower head, they were distributed regularly in the bud and never fed in the same spot. Third-instar larvae fed on achenes and receptacle tissues. Upon completion of feeding, each larva constructed a cocoon cell from the chewed pappus, in which it formed the puparium. The larvae and puparia were anchored with the apical end in the receptacle and the caudal end pointing upwards. Adults of the first generation emerged in summer and soon mated and laid their eggs. In central Europe, larvae of a second or a possible third generation, that reached their full size in early autumn ceased development after they completed their cocoon cells. The diapausing overwintering larvae initiated pupariation only in the first half of the following April. The pupal stage lasted until the second week of May, when the first adults emerged. The mortality of larvae and pupae were not recorded, but larvae were apparently killed by endoparasites, predators, and especially by birds during winter.

Precopulatory behavior.—Adults of *C. cylindrica* meet on the larval food plant. Males appear to respond to any movement in their vicinity. If they observe another in-



Figs. 13–18. Puparium. 13, Ventral view. 14, Thoracic segments, ventral view, ribbed pattern. 15, Puparium, lateral view. 16, Thoracic segments, lateral view. 17, Puparium, anterior part bearing anterior thoracic spiracles. 18, Anterior thoracic spiracles.

sect of similar size at a distance of ca. 5 cm, the male fly will flick their wings, probably in an attempt to scare the intruder off. Male–male encounters were observed five times. Upon recognizing a conspecific rival, a male tried to push the other from the plant and performed quick enantion (see below)

wing displays. Rivals pushed each other with their heads, and batted each other with their forelegs and flicking their wings. In two cases, males initiated copulation, and after failing they fought until one was chased away.

Females were observed to walk on the



Figs. 19–22. Puparium. 19, Caudal segment with posterior spiracular plates. 20, Caudal segment with posterior spiracular plate with rimae and interspiracular processes. 21, Emergence from pupa. 22, Emergence from pupa, detail with anterior thoracic spiracles.

tops of plants with their wings stretched apart and ovipositor extruded. When meeting a female, a male soon tried to copulate, but usually they first exhibit precopulatory behavior without direct body contact. A study of 5 pairs in the field and 20 in the laboratory showed that the period of precopulatory behavior is short from 1–10 minutes. During courtship a male and a female walked in tandem or facing each other, or they moved around each other without any apparent pattern (observed in 7 pairs in the field and 2 in the laboratory). Body swaying was a typical component of the precopulatory behavior in both sexes. The female also performed cleaning movements; with the forelegs she brushed her head, especially the eyes and mouthparts, and with the hind legs she brushed the wings and abdomen.

Courtship and mating.—Precopulatory behavior was followed by male attempts to mount females. Female receptivity was manifested by raising her ovipositor and by frequent wing movements. A male mounted on a female's back and grasped her aculeus with his surstyli and prensisetae. The intromission of the aculeus into the cloacal opening followed. A male pressed, with his hind pair of legs, the female pregenital abdominal segments against his epandrium and sometimes stroked the female's abdomen with their midlegs. In five observations, females stroked their own abdominal segments with their midlegs. The male forelegs grasped the female's mesoscutum during copulation. Females waved or flicked their wings, brushed their heads with their forelegs and slowly walked on the plant. Males periodically repeated the copulatory

movements. Pairs remained in copulation for up to 3 hours, if not interrupted. Males eventually dismounted females, turned 180° and walked away in the opposite direction allowing the genitalia to disengage. Observations on 15 pairs in nature and 5 in the laboratory revealed that both males and females copulate more than once in their lifetime.

Oviposition behavior.—Females oviposit into closed buds 9–14 mm in diameter ($n = 300$), but most often 12 mm (243 buds). Females first inspected whether the bud already has been infested walking around it, rubbing the bracts with their forelegs and touching them with their mouthparts. Females abandoned buds that were later verified by dissection to be previously occupied or were otherwise unsuitable for oviposition ($n = 5$). If a female accepted a bud, she inserted her aculeus between the bracts and in between the underlying florets. When inserting her ovipositor into the flower head, a female stood on the involucre bract not facing the bud as is usual in other fruit fly species (Headrick and Goeden 1994) but with her head directed away. The abdomen and the ovipositor formed a straight line with the head and thorax. Oviposition episodes observed in the field lasted up to 3 minutes and usually only a single egg was laid during each ovipositor insertion. Eggs were inserted with the posterior end first, while the anterior end bearing the micropyle and pedicel was protected against mechanical damage (see Figs. 1–2). Females oviposited repeatedly (in 15 out of 20 observed females) into the same bud. Following oviposition, females walked around the flower heads with their ovipositors exposed (2 of 20 females). This behavior resembled pheromone marking known for other tephritids, which deposit pheromones to deter other female from oviposition (Prokopy and Roitberg 1984). Oviposition is terminated with slow retraction of the ovipositor and its cleaning with the hind legs.

Wing displays.—*Chaetostomella cylin-*

drica has a banded wing pattern similar to many other fruit flies. Displays of this pattern play a role in precopulatory behavior—to attract a female or to deter conspecific males and other intruders—and provide defense against predators, especially spiders of the families Lycosidae and Salticidae that jump to catch their prey. Some fruit flies, including *C. cylindrica*, resemble these spiders and use this camouflage to avoid spider attacks (Greene et al. 1987, Mather and Roitberg 1987). Even during copulation when a male was engaged, females waved their wings to deter possible intruders and predators. The wing displays of fruit flies were classified into five categories by Headrick and Goeden (1994), of which enantion, supination, and hamation occur in both sexes of *C. cylindrica*. Enantion is a simultaneous extension of both wings away from the body. Supination is a common wing maneuver and consists of bringing the wing forward perpendicular to the long axis of the body, while the ventral surface of the wing is turned anterior so that the costa is dorsal. Hamation is a simultaneous movement of the wings from side-to-side.

Trophallaxis.—Both males and females were observed with a drop of liquid on their mouthparts during precopulatory behavior and during other activities, but direct contact of two individuals with their labella and transmission of the fluid was not observed. Trophallaxis in form of a nuptial gift is a component of the precopulatory behavior in many species of tephritids (Freidberg 1982); in the genus *Chaetostomella* it is recorded here for the first time.

Phenology and Host Plants

Adults of *C. cylindrica* first appeared in 2002 in northwestern Bohemia on May 11 and in central Bohemia on May 1. The last adults were collected on August 27 and 20, respectively, indicating that in central Europe the larvae enter diapause at the beginning of August. Flies were swept near Prague on various plants (*Centaurea sca-*

biosa L., *Centaurea jacea* L., *Centaurea cyanus* L., *Arctium lappa* L., *Cirsium oleraceum* (L.) Scop., and *Cirsium palustre* (L.) Scop.) and were reared from flowerheads of *C. jacea*, *C. pseudophrygia*, *C. oleraceum*, and *C. canum* (L.) All. Two generations were reliably observed in 2002, and several adults of a third generation were caught in the second half of August in 2003. Merz (1994) and White (1988) reported occurrence of one or two generations per year in the climatic conditions of central Europe, but our data demonstrate that there may be one more. The two years of our study differed significantly in average temperature during the summer months and in the amount of rainfall. The year 2002 was extremely cold and rainy, while 2003 was very hot and dry. The results show that *C. cylindrica* can produce an increased number of generations per year when the climate is suitable and a host plant is available.

Since a maximum of three larvae of *C. cylindrica* develop in a flowerhead, only three achenes are directly destroyed. Seed reduction thus seems to be very limited, but we know nothing about the developmental capacity of the remaining achenes. It is possible that feeding of the larvae on the receptacle may restrain the flow of nutrients and thereby reduce seed fitness. The germination potential and the survival of seedlings must be measured before we can assess the impact of *C. cylindrica* on knapweed. Several other features of *C. cylindrica* biology are important to consider for the possible use of this species for biological control of weeds. The ability of developing larvae of *C. cylindrica* to share the flowerhead with larvae of other fruit fly species and the larvae of beetles may be advantageous. For example, *C. cylindrica* could attack knapweeds and thistles contemporaneously with *Urophora quadrifasciata* (Meigen) in the USA. The ability of *C. cylindrica* to develop in a variety of weeds is usually also an advantage, but whether it would attack native plants is a danger that must be taken into account. The polyphagy

of *C. cylindrica* makes its use in biological control somewhat risky because the family Asteraceae is very diverse and some species of the family occur at the same localities and at the same time as the target weeds. In central Europe, however, *C. cylindrica* develops exclusively in knapweeds and thistles.

ACKNOWLEDGMENTS

We are very indebted to Dr. M. Chvála, Charles University, Praha, for comments on the manuscript, and Dr. B. Merz, Muséum d'Histoire Naturelle Genève for help with the determination of problematic specimens and donation of comparative material to the Charles University collection. We thank Mrs. J. Hromádková, Laboratory of the Institute of Macromolecular Chemistry, Academy of Sciences of the Czech Republic, for the SEM work and Mr. Russell Blake Praha for linguistic correction. The study was supported by a grant of the Ministry of Education (MŠMT ČR J13/98113100004).

LITERATURE CITED

- Dirlbek, J. 1970. Beitrag zur Erkennung der Eier, Larven und Puppen einiger Arten von Bohrflieden (Diptera, Trypetidae) aus dem Gebiet der Westlichen Karpaten. Biologické základy polnohospodárstva 8: 155–168.
- Freidberg, A. 1982. Courtship and post-mating behaviour of the fleabane gall fly, *Spathulina tristis* (Diptera: Tephritidae). Entomologica Genalis 7(4): 273–285.
- Freidberg, A. and J. Kugler. 1989. Diptera: Tephritidae. Fauna Palestina—Insecta IV. Keterpress Enterprises, Jerusalem, Israel.
- Greene, E., L. J. Orsak, and D. W. Whitman. 1987. A tephritid fly mimics the territorial displays of its jumping spider predators. Science 236: 310–312.
- Harris, P. and J. H. Myers. 1984. *Centaurea diffusa* Lam., and *C. maculosa* Lam. s. lat., diffuse and spotted knapweed (Compositae), pp. 127–137. In Kelleher, J. S. and M. A. Hulme, eds., Biological control programmes against insects and weeds in Canada 1969–1980, Commonwealth Agricultural Bureaux.
- Headrick, D. H. and R. D. Goeden. 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera)

- mating systems. *Studia Dipterologica* 1(2): 194–252.
- Hendel, F. 1927. Trypetidae, pp. 1–221. *In* Lindner, E., ed. *Die Fliegen der palaearktischen Region*. 49. Lieferung 16–19, Schweizerbart, Stuttgart.
- Kinkorová, J. 1999. What do we know about Czech and Slovak Tephritidae (Diptera)? *Dipterologica bohemoslovaca* 9: 89–95.
- Kinkorová, J. and M. Chvála. 2000. Critical review of the subfamily Terelliinae (Diptera: Tephritidae) in Central Europe. *Acta Universitatis Carolinae-Biologica* 44: 133–155.
- Kugler, J. and A. Freidberg. 1975. A list of the fruit flies (Diptera: Tephritidae) of Israel and nearby areas, their host plants and distribution. *Israel Journal of Entomology* 10: 51–72.
- Kubát, K., L. Hrouda, J. Chrtek jun., Z. Kaplan, J. Kirchner, and J. Štěpánek, eds. 2002. *Klíč ke květeně České Republiky*. (Key to the Flora of the Czech Republic). Academia, Praha.
- Leclercq, M. 1967. Contribution à l'étude des Trypetidae (Diptera) paléarctiques et de leurs relations avec les végétaux. *Bulletin of Recherche Agronomie Gembloux*. N.S. II. 64–105.
- Mather, M. H. and B. D. Roitberg. 1987. A sheep in wolf's clothing: Tephritid flies mimic spider predator. *Science* 236: 308–309.
- Merz, B. 1994. *Diptera, Tephritidae*. *Insecta Helvetica, Fauna* 10. Genève.
- Norrbom, A. L., L. E. Carrol, and A. Freidberg. 1998a. Status of knowledge, pp. 9–48. *In* Thompson F. C., ed. *Fruit fly expert identification system and biosystematic information database*. *Myia*, 524 pp.
- Norrbom, A. L., L. E. Carrol, F.C. Thompson, I. M. White, and A. Freidberg. 1998b. Systematic database of names. Status of knowledge, pp. 65–524. *In* Thompson F. C., ed. *Fruit fly expert identification system and biosystematic information database*. *Myia*, 524 pp.
- Prokopy, J. R. and B. D. Roitberg 1984. Foraging behavior of true fruit flies. *American Scientist* 72: 41–49.
- Richter, V. A. 1970. 62. Tephritidae (Trypetidae), pp.132–172. *In* Bei-Bienko G. Ja., ed. *Keys to the Insects of the European Part of the USSR*. *Opre-delitel Faune SSSR* 103(V).
- Steck, G. J. 1984. *Chaetostomella undosa* (Diptera: Tephritidae): Biology, ecology, and larval description. *Annals of the Entomological Society of America* 77: 669–678.
- Thompson, F. C. 1998. *Fruit Fly Expert Identification System and Systematic Information Database*. *Myia*, Leiden 9, 524 pp.
- Tutin, T. G. 1976. *Flora Europea*, Vol. 4. *Plantaginaceae to Compositae and Rubiaceae*. xxix-1505. Cambridge University Press, New York.
- Varley, G. C. 1937. The life history of some tephritid flies with description of the early stages (Diptera). *Proceedings of the Royal Entomological Society London (A)* 12: 109–122.
- White, I. M. 1988. *Tephritid Flies (Diptera, Tephritidae)*. *Handbooks for the Identification of British Insects* 11 (part 5a). Dorset Press, London.
- White, I. M. and M. M. Elson-Harris. 1992. *Fruit Flies of Economic Significance: Their Identification and Bionomics*. CAB International, London.